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FURTHER OBSERVATIONS ON THE BIOLOGY AND HOST SPECIFICITY OF *PROCHOERODES TRUXALIATA* (GUENÉE) (LEPIDOPTERA: GEOMETRIDAE), A BIOLOGICAL-CONTROL AGENT FOR *BACCHARIS HALIMIFOLIA* L. IN AUSTRALIA

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Abstract.—Studies on the developmental and reproductive biology of *Prochoerodes truxaliata* (Guenée) were conducted on *Baccharis pilularis* de Candolle at Davis, California. Under laboratory conditions, mean developmental time from egg to adult was slightly shorter for males (49 days) than for females (50.6 days). Developmental times for fourth and fifth instar larvae and for pupae were significantly different between sexes. Mean generation time for females was approximately 53 days. There were five larval instars and measurement of head capsules revealed a relatively constant growth ratio (0.64–0.68). Longevity of adults was approximately 10 days. Following a short preoviposition period (approximately two days), females which laid fertile eggs produced an average of 489 eggs per female; however, not all the eggs were always deposited prior to the death of a given female. Other females, despite their exposure to males, laid only infertile eggs; however, total number of eggs produced per female was lower than that observed for fertile females ($\bar{x} = 339$) and only one third of these were actually deposited. Field observations revealed that moths which were active early in the evening laid predominantly fertile eggs, whereas those active later in the evening laid predominantly infertile ones. In quarantine facilities in Australia, host specificity of larvae was tested on a wide range of economic and native plant species unavailable in the U.S. Larvae fed on a number of asteraceous plants but were unable to complete development on any plant other than *Baccharis halimifolia* L. Consequently, *P. truxaliata* has been cleared for release in Australia for control of *B. halimifolia.*

Key Words.—Insecta, Lepidoptera, Geometridae, *Prochoerodes truxaliata,* biological control/weeds, *Baccharis*

There are over 200 species of insects associated with *Baccharis pilularis* de Candolle in California (Tilden 1951). This insect fauna has been of considerable ecological interest over the years, and more recently certain species in the community attained practical importance in biological control. A related host plant, *Baccharis halimifolia* L., which is native to the southeastern U.S., is a serious, introduced rangeland weed in Australia. During foreign exploration for natural enemies of *B. halimifolia* in the U.S., it was discovered that a number of species previously recorded only from *B. pilularis* would also feed and complete development on *B. halimifolia* (WAP, unpublished data). At least two were sufficiently stenophagous to permit their importation into Australia. The cecidomyiid midge *Rhopalomyia californica* Felt, which develops in conspicuous terminal galls on *B. pilularis,* was introduced into Queensland in 1982; it established, and by 1986 had spread throughout the range of the target weed (McFadyen 1985; WAP, unpublished data). The second species, *Prochoerodes truxaliata* (Guenée), is one of the least conspicuous insects associated with *B. pilularis* in California. The cryptic larvae of this geometrid can cause severe defoliation and thus this species shows considerable promise as a biological-control agent.

The pre-introductory investigations required for clearing *P. truxaliata* for importation into Australia resulted in a considerable amount of new information on this rather poorly known species. Palmer & Tilden (1987) reported on its developmental biology and host specificity; the latter studies involved plants available in the U.S. (primarily Texas), including native species. This paper reports additional data on developmental and reproductive biology of *P. truxaliata,* and the results of host-specificity tests conducted in Australia.

Materials and Methods

Laboratory Studies.—The insects used in the laboratory studies were the progeny of 20 female moths collected from *B. pilularis pilularis* on the Davis campus of the University of California (Solano County). The moths were held in a sleeve cage in the laboratory and observed daily for oviposition. Eggs were collected each day and placed in ventilated microcentrifuge tubes. One cohort of eggs was stored at 5° C for 18 days before being placed in the rearing room, whereas all other eggs were immediately placed in the rearing room and held at 25° C. The eggs held in cold storage were a subset of those eggs allowed to accumulate in storage prior to shipment to Australia for use in host-specificity tests. During incubation, all eggs were observed several times daily and the date and time of eclosion were recorded for each larva.

Newly hatched larvae were transferred to rearing chambers constructed from 30 ml plastic containers and held at 25° C (one larva per chamber). A circular hole (one cm diameter) was cut in the bottom of the container and covered with 90-mesh nylon organdy. The severed end of a cutting taken from a growing tip of *B. p. pilularis* from the Davis campus was inserted through a small hole in the lid of the plastic cup so that about one cm of stem protruded. The lid was placed on the cup, the entire unit was inverted, and then allowed to float on styrofoam in a tray of distilled water allowing the stem of the cutting to remain submerged. As larvae grew larger, these containers were replaced with 60 ml plastic containers of similar construction. Rearing chambers were cleaned and fresh foliage was added daily. Larvae were observed several times a day and behavioral activities were noted.

A minute droplet of silver conducting paint (Ladd Research Industries, Inc., stock number 60805) was placed on the dorsal surface of the head of the newly hatched larva. This was repeated after each molt and the head capsules were later recovered for each successive instar. The sequence of head capsules for each larva was then glued to a microscope slide; each capsule was measured at 50× using a Nikon stage micrometer electronically wired to an Autometronics dual-axis digital readout. Measurements were expressed in millimeters.

Pupae were sexed and held in the rearing room until emergence. As the moths emerged, individual male/female pairs were confined in 450 ml plastic cylindrical containers. The bottom of the container was removed and replaced with a double-weave brass screen. One mm-square openings in the screen permitted the 0.8 mm eggs to drop through, and into a collecting tray beneath the unit. A circular hole was cut in the lid of the container and replaced with 90-mesh nylon organdy. A cotton wick saturated with 20% sucrose solution was inserted through a hole in the side of the cage. Eggs were collected daily and held in ventilated microcentrifuge tubes at 25° C for determination of fertility. Moths were observed daily,

and dead individuals were removed. Shortly after death, females were dissected in physiological saline solution and the condition of the reproductive tract and the number of eggs remaining was recorded.

Field Observations.—Moth behavior was observed in the campus arboretum during the evenings of 11–12 Jul 1988. On each night, moths were observed and captured during two intervals: 20:30–22:10 h and 23:00–00:10 h. Observations were terminated shortly after midnight due to the general absence of active female moths. Behavior of moths was observed with the aid of a flashlight. All females were returned to the laboratory, held individually in 60 ml plastic containers, and observed for oviposition. Egg fertility was recorded for each female.

Host Specificity.—In the quarantine laboratory at the Alan Fletcher Research Station (Sherwood, Qld., Australia), all plants listed in Table 1 were tested against neonate larvae. A leaf of each plant was selected and examined to ensure that there was no insect damage. It was then placed in a plastic petri dish with five newly hatched, unfed larvae. The larvae used in this and subsequent experiments were obtained from eggs shipped directly to Australia from Davis. The source population was the same as that used in the laboratory studies. Every two days the contents of the dishes were examined and the foliage replaced. Live larvae, frass, head capsules or feeding marks on the leaf were noted. Three replications of each plant species were made. The tests were conducted in randomized batches of 20 plants which always included *B. halimifolia* as a control.

Eighteen species were selected from those in Table 1 to ascertain whether larvae behaved similarly on potted plants and on cut foliage. The selection included all the Astereae and a random selection of other species. Five neonate larvae were placed on foliage of each plant; a fine-mesh bag was placed over them to confine them to a portion of the plant. The plants were placed in a greenhouse, examined at regular intervals, and the surviving larvae noted. The experiment was replicated twice.

A test was also conducted to determine whether late-instar larvae had a wider host range than neonate larvae. In this test, which was replicated twice, all the species in the Asteraceae in Table 1 were used. Larvae were reared from eclosion on *B. halimifolia* foliage until they were estimated to be third instar. Five larvae were then transferred to cuttings of a test plant held in souffle cups filled with water. These cuttings were then placed individually in 500 ml plastic containers. The contents of the containers were then examined regularly and live larvae, frass, exuviae and feeding damage noted. The foliage was replaced every three days.

Results and Discussion

Laboratory Studies.—Our observations of the eggs of *P. truxaliata* were generally similar to those of Palmer & Tilden (1987). The egg is nearly spherical (slightly ovoid), and approximately 0.8 mm in diameter. The chorion is glossy with a textured surface, and has no known adhesive substances. The newly deposited egg is turquoise green. The fertile egg turns brown after about 48 h (some may require up to 72 h), whereas an unfertile egg retains its original color. As it hatches, the first instar larva chews a circular opening in the chorion. The chorion is seldom if ever eaten by the larva. Mean developmental time for eggs was approximately 10 days at 25° C, with no significant difference between males and females (Table 2). In contrast, chilled eggs (at 5° C for 18 days prior to incubation

Table 1. The plants against which neonate larvae were tested in the cut foliage, no-choice experiment.

Anacardiaceae: *Mangifera indica* L.
Apiaceae: *Apium graveolens* L.
Asteraceae: Tribe Astereae: *Aster novi-belgii* L., *Brachycome multifida* de Candolle, *Callistephus chinensis* (L.) Nees Von Esenbeck, *Calotis cuneata* (F. Mueller ex. Bentham) G. L. Davis, *Conyza sumatrensis* (Retzius) E. H. Walker, *Olearia nernstii* F. Mueller, Bentham, *Vittadinia sulcata* N. T. Burbidge. Tribe Heliantheae: *Cosmos bipinnatus* Cavanilles, *Dahlia variabilis* (Willdenow) Desfontaines, *Eclipta prostrata* (L.) L., *Gaillardia aristata* Pursh, *Glossogyne tenuifolium* Cassini, *Helianthus annuus* L., *Wedelia biflora* de Candolle, *Zinnia linearis* Bentham. Tribe Inuleae: *Cassinia laevis* R. Brown, *Gnaphalium sphaericum* Willdenow, *Helichrysum bracteatum* (Ventenat) Andrews. Tribe Senecioneae: *Emilia sonchifolia* (L.) de Candolle, *Flaveria australasica* Hooker, *Senecio lautus* Solander, ex. Willdenow. Tribe Anthemideae: *Chrysanthemum carinatum* Schousboe, *Cotula australis* (Sieber) Hooker f. Tribe Eupatorieae: *Adenostemma lavenia* (L.) Kuntze. Tribe Vernonieae: *Vernonia cinerea* (L.) Lessing. Tribe Lactuceae: *Cichorium intybus* L. Tribe Cynareae: *Carthamus tinctorius* L. Tribe Calenduleae: *Calendula officinalis* L.
Brassicaceae: *Brassica oleracea* L.
Caricaceae: *Carica papaya* L.
Chenopodiaceae: *Beta vulgaris* L.
Cucurbitaceae: *Cucurbita maxima* Duchesne
Fabiaceae: *Arachis hypogaea* L., *Medicago sativa* L., *Phaseolus vulgaris* L.
Liliaceae: *Allium cepa* L.
Malvaceae: *Gossypium hirsutum* L.
Myrtaceae: *Eucalyptus* sp.
Passifloraceae: *Passiflora edulis* J. Sims
Poaceae: *Triticum aestivum* L., *Saccharum officinarum* L., *Sorghum vulgare* Persoon, *Zea mays* L.
Proteaceae: *Macadamia integrifolia* J. Maiden & E. Betche
Rosaceae: *Fragaria vesca* L.
Rubiaceae: *Coffea arabica* L.
Rutaceae: *Citrus sinensis* (L.) P. Osbeck
Solanaceae: *Solanum tuberosum* L., *Lycopersicon lycopersicum* L.
Vitaceae: *Vitis vinifera* L.

at 25° C) hatched at least three days sooner. Such an effect has been documented in other insects (Lin et al. 1954, Kimberling & Miller 1988). In such cases, although the insect's embryonic development evidently continues at temperatures below the thermal threshold for eclosion, the entire developmental sequence leading to larval eclosion cannot be completed. This finding may be helpful in the mass production and colonization of *P. truxaliata,* particularly when cold storage of eggs is necessary. However, the eclosion rate among chilled eggs was considerably less (54%, $n = 69$) than for non-chilled eggs (78.1%, $n = 170$).

Larval eclosion occurred between dusk and dawn. The neonate larva actively searched the host plant and generally displayed a negative geotropism (also noted by Palmer & Tilden 1987). When given a choice, the larva fed on young leaves in the meristematic region. In the absence of such leaves, the larva would feed on well developed leaves and showed a marked preference for younger foliage. As noted by Palmer & Tilden (1987), first instar larvae (in contrast to later instar larvae) commonly fed during the day in addition to nocturnal feeding. When resting, the smaller larva assumed an erect position, mimicking defoliated petioles; larger larvae mimicked small twigs. The larva held the substrate with its prolegs

Table 2. Developmental times and head-capsule widths for *P. truxaliata* in the laboratory.

Stage	Developmental time (days)[a] Mean ± SEM[c] Male		Mean ± SEM[c] Female	Range Male	Range Female	Mean (± SEM)[b] head-capsule width (mm)[c] Male		Mean (± SEM)[b] head-capsule width (mm)[c] Female
Egg	9.63 ± 0.09		9.60 ± 0.09	9–10	9–10	–		–
1st instar	4.81 ± 0.18		4.63 ± 0.21	4–7	4–7	0.430 ± 0.003		0.429 ± 0.003
2nd instar	4.66 ± 0.2		4.43 ± 0.11	3–8	3–6	0.656 ± 0.005		0.659 ± 0.006
3rd instar	4.41 ± 0.19		4.33 ± 0.23	3–7	3–8	1.025 ± 0.014		1.039 ± 0.01
4th instar	4.47 ± 0.14	*	5.23 ± 0.14	3–6	4–7	1.541 ± 0.01	*	1.611 ± 0.011
5th instar								
Active	6.66 ± 0.17	*	8.67 ± 0.32	5–9	6–14	2.294 ± 0.033		2.363 ± 0.043
Prepupa	2.25 ± 0.13		2.43 ± 0.11	1–4	1–3	–		–
Pupa	12.16 ± 0.2	*	11.33 ± 0.22	10–14	8–13	–		–
Egg to adult	48.97 ± 0.63		50.6 ± 0.75	42–58	44–60	–		–

[a] Based on 32 male and 30 female individuals which completed development to adult.
[b] Based on 17 male and 19 female individuals which completed development to adult.
[c] Asterisk indicates significant difference (t-test, $P \leq 0.05$).

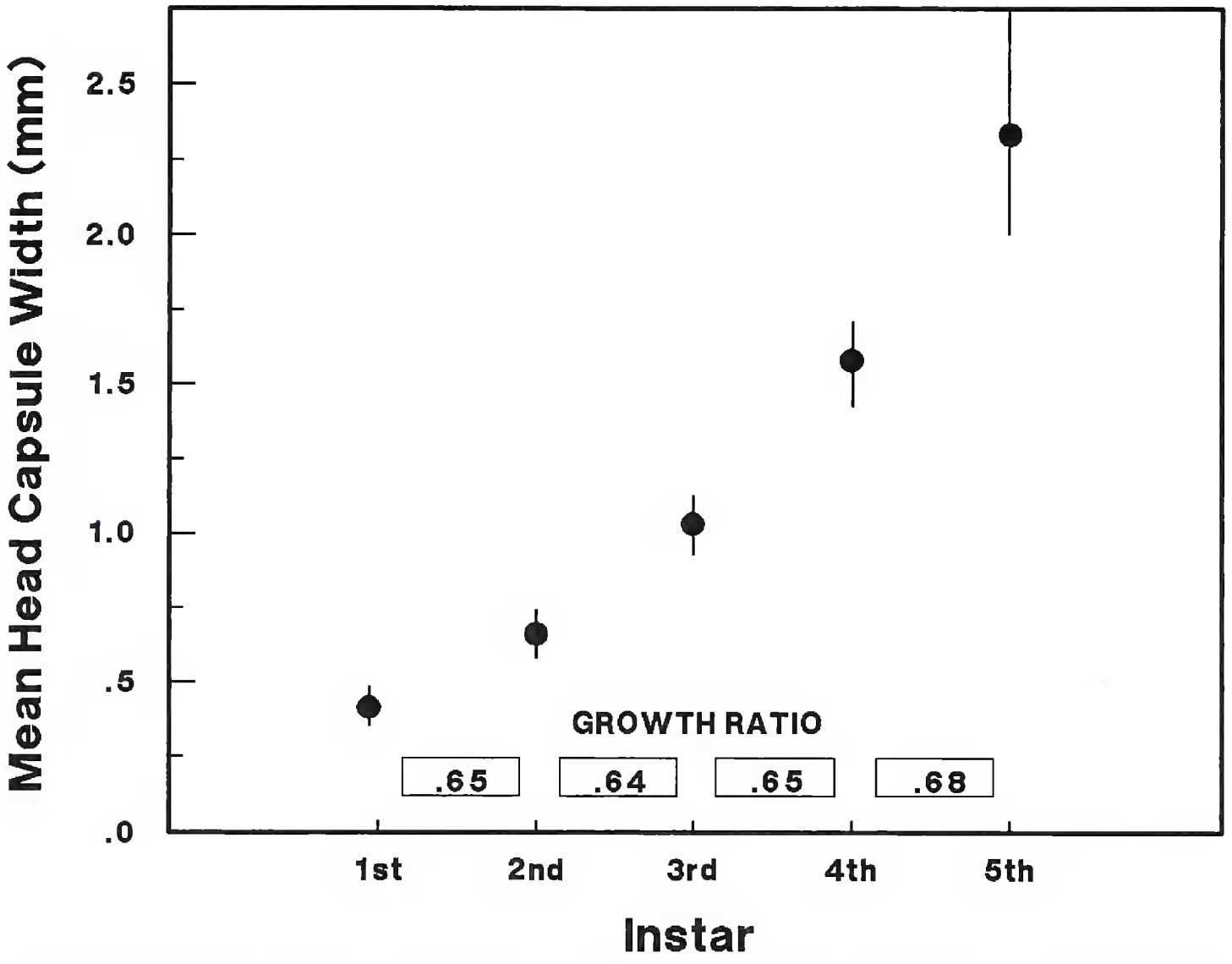

Figure 1. Mean and range of head-capsule widths for the five larval instars of *P. truxaliata* (data from both sexes).

and assumed a 45° angle to the stem. This position was maintained with the aid of a silken strand, from the spinnerettes, also attached to the stem. The larva would drop when disturbed, and remain suspended from the foliage by the silken strand. Mean developmental time for first-instar larvae was slightly less than five days and did not vary with sex (Table 2).

Subsequent instars were nocturnal feeders. Second and third instar larvae showed a similar preference for young leaves in the meristematic region and when disrupted, dropped from the plant as did the first instar. Mean developmental times for these instars were approximately the same and did not vary with sex (Table 2). For fourth instar larvae, however, mean developmental time for males was significantly shorter than for females; that for females was almost one day longer than for females of the third instar (Table 2). Both fourth and fifth instar larvae behaved differently than previous instars by showing less preference for younger leaves, and not readily dropping from the plant when disturbed.

The fifth instar consisted of an active feeding phase followed by a non-feeding prepupal period. Mean developmental time for the active phase was the longest for any instar, and that for the males was significantly shorter than for females (Table 2). The prepupal period lasted slightly more than two days and did not vary with sex (Table 2). During this period, a silken structure was spun which eventually housed the pupa. The pupal stage was significantly shorter for females

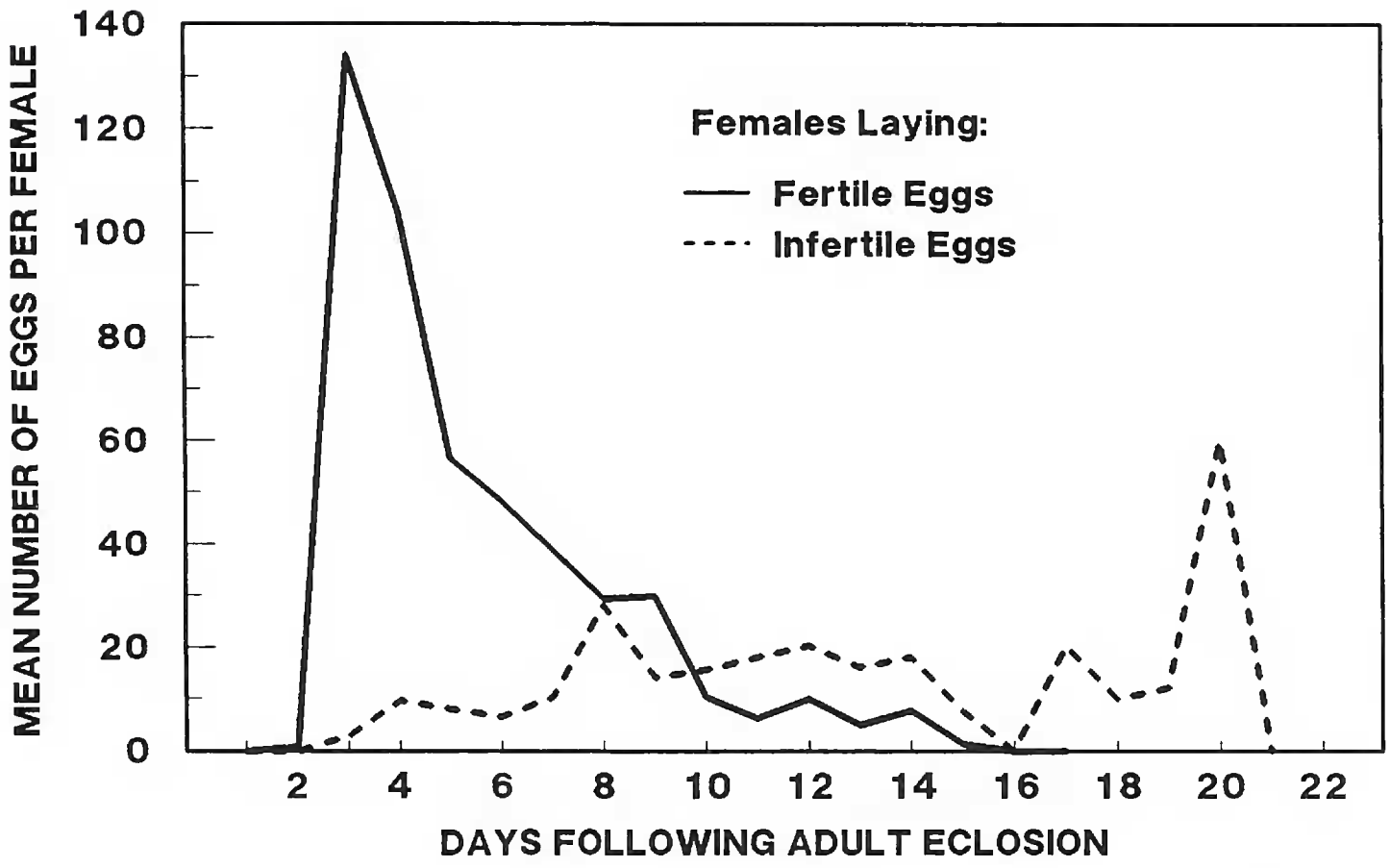

Figure 2. Mean number of eggs laid per female per day for *P. truxaliata* under laboratory conditions.

than for males. Sexual dimorphism, expressed in the terminal abdominal segments, was sufficient to enable sorting of pupae according to sex.

The average head-capsule widths for the five instars were consistent with the "Brooks-Dyar Rule" (cf. Daly 1985). With the exception of fourth instar larvae, there was no significant difference between sexes (Table 2). Average values incorporating data from both sexes are plotted in Fig. 1. There is no overlap among the instars and thus head-capsule width would appear to be a suitable indicator of instar in field collections. The range for fifth instar larvae was relatively large. We attribute this to the fact that dorsal sutures of these head capsules seldom remained intact; this caused difficulty in obtaining accurate measurements. The growth ratio was relatively constant (0.64–0.68) and is generally consistent with previous studies of lepidopterous larvae (Drooz 1965, Dupree 1965, Enders 1976). In two cases, we observed six instars, but neither survived to adulthood. Palmer & Tilden (1987) reported up to seven and sometimes eight instars in this species. This is not particularly surprising, as number of instars in Lepidoptera can vary according to environmental conditions (Long 1953).

Mean developmental time from egg to adult was slightly longer for females (50.6 days) than males (49 days) (Table 2). Adults eclosed and were active only at night. Adult longevity for males (10.7 days) was higher (not significant) than for females (9.6 days). Following a 2–3 day preoviposition period in the laboratory, two groups of females were evident: fertile versus unfertile. Fertile females laid approximately 50% of their eggs within the first four days (Fig. 2), averaging 445.7 ($n = 13$) eggs per female. However, dissections revealed that an average of 42.9 eggs per female remained in the reproductive system at death. Thus, the total potential fecundity per fertile female was considered to be 488.6. Infertile females laid a relatively constant number of eggs per female per day (Fig. 2), but the total

Table 3. Percent survival of neonate larvae at 7 and 21 days on those plants on which any survival was observed at 7 days.

Plant species	% survival	
	7 days	21 days
Baccharis halimifolia	82	70
Callistephus chinensis	73	0
Calotis cuneata	27	0
Cotula australis	40	0
Eclipta prostrata	27	6
Vittadinia sulcata	13	0

eggs deposited per female was approximately 25% (average 110.2, $n = 12$) of that for fertile females. Furthermore, nearly twice as many eggs remained in the reproductive system at the time of death (average 228.5) as were deposited and many unlaid eggs were undeveloped. Total potential fecundity for these females averaged 338.7. We cannot explain why infertile females, despite being given the same opportunity to mate, failed to deposit fertile eggs. Average longevity of fertile and infertile females did not differ significantly.

Field Observations.—Moths which were active (readily visible in the upper strata of the foliage) early in the evening laid predominantly fertile eggs whereas those active later in the evening laid predominantly infertile eggs. Thirty-seven of 41 females (90.2%) collected between 20:30 and 22:00 h laid eggs prior to the fourth day after capture. Virtually all of the eggs for each female were fertile. Thirty-three of the 37 moths (89.2%) laid eggs prior to dawn of the following day, indicating the moths had mated at least one day prior to capture. The remaining

Table 4. Percent survival of neonate larvae on foliage of potted plants.

Plant species	% survival		
	Week 1	Week 4	Week 8
Allium cepa	0	—	—
Arachis hypogaea	0	—	—
Aster novi-belgii	0	—	—
Baccharis halimifolia	60	60	60
Brachycome multifida	0	—	—
Callistephus chinensis	20	20	0
Calotis cuneata	0	—	—
Cassinia laevis	10	0	—
Conyza sumatrensis	0	—	—
Cosmos bipinnatus	0	—	—
Cotula australis	10	0	—
Cucurbita maxima	0	—	—
Eclipta prostrata	0	—	—
Gossypium hirsutum	0	—	—
Helichrysum bracteatum	0	—	—
Olearia nernstii	10	—	—
Vernonia cinerea	0	—	—
Vittadinia sulcata	30	20	0
Zinnia linearis	0	—	—

Table 5. Percent survival when 3rd instar larvae were placed on bouquets of foliage.

Plant species	% survival		
	Week 1	Week 3	Week 6
Adenostemma lavenia	0	—	—
Baccharis halimifolia	100	80	40
Brachycome multifida	20	0	—
Calendula officinalis	0	—	—
Callistephus chinensis	10	0	—
Calotis cuneata	10	0	—
Carthamus tinctorius	10	0	—
Cassinia laevis	40	20	0
Chrysanthemum carinatum	0	—	—
Cosmos bipinnatus	0	—	—
Cotula australis	60	0	—
Dahlia variabilis	10	0	—
Eclipta prostrata	20	0	—
Emilia sonchifolia	0	—	—
Gaillardia aristata	0	—	—
Glossogyne tenuifolium	20	10	0
Gnaphalium sphaericum	30	0	—
Helianthus annuus	10	0	—
Helichrysum bracteatum	0	—	—
Olearia nernstii	20	0	—
Senecio lautus	10	0	—
Vernonia cinerea	20	0	—
Vittadinia sulcata	0	—	—
Wedelia biflora	10	0	—
Zinnia linearis	10	0	—

four females oviposited but none of their eggs hatched. All of the 28 females collected between 23:00–00:10 h laid eggs, although only 12 (42.9%) laid predominantly fertile eggs. None of the eggs of the remaining 16 females were fertile. Males and females were caught in a one-to-one sex ratio. Apparently virgin females are active later in the evening, presumably seeking mates; once mated, they become active earlier in following evenings. This hypothesis, however, should be tested further.

Host Specificity.—After seven days, neonate larvae placed on cut foliage of most of the plants listed in Table 1 had died without any appreciable feeding. However, surviving larvae and evidence of feeding were found on five species (Table 3). By the end of three weeks, all larvae except one on *Eclipta prostrata* (L.) L. had died. This individual remained alive for 12 more days, although it developed at a much slower rate than control larvae on *Baccharis.* No larvae (other than the controls) survived longer than 33 days, nor did any complete development.

Neonate larvae placed on potted plants survived for less than a week on all but five species. Three of these species [*Callistephus chinensis* (L.) Nees Von Esenbeck, *Cotula australis* (Sieber) Hooker f., and *Vittadinia sulcata* N. T. Burbidge] were common to those supporting larvae for a week in the cut-foliage experiment (Table 4). On these five, there was evidence of feeding and development to at least the second instar. On only *Callistephus chinensis* was the growth rate similar to that

observed on *B. halimifolia.* The larvae on *C. chinensis* grew rapidly through the first three instars but then ceased development and died three weeks later. The increased mortality and the failure of the surviving larvae to develop indicate that this plant is not a suitable host.

Late instar larvae could not complete their life cycle on cut foliage of any of the test plants (Table 5). In many cases the larvae took longer than a week to die, even if they did not feed. On only two plants, *Cassinia laevis* R. Brown and *Glossogyne tenuifolium* Cassini, was there any protracted feeding. On these, however, there was negligible growth of the larvae and they eventually died.

This insect exhibited an ability for early instar larvae to feed on a number of Asteraceae, almost all in the tribe Astereae and thus has been comprehensively tested. In the United States and Australia, it has been tested against plants in (1) 12 genera of the Astereae (approximately 10% of the genera of this tribe throughout the world) and (2) 31 genera in other tribes of the Asteraceae (see also Palmer & Tilden 1987). This testing against closely related plants is one of the most comprehensive of any insect candidate for biological-control. All the evidence gathered indicates that *P. truxaliata* is host-specific to certain *Baccharis* spp. In addition, there is no record in the United States of it ever being found on any plant other than a *Baccharis* spp. Because host-specificity experiments indicated that *P. truxaliata* was able to utilize only *Baccharis* spp., it was considered safe to release in Australia. Permission for release from quarantine was granted in February, 1989.

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